BIOSYSTEMATICS OF PSILOSTROPHE (COMPOSITAE: HELENIEAE). II. ARTIFICIAL HYBRIDIZATION AND SYSTEMATIC TREATMENT

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Psilostrophe comprises seven species that grow in the semiarid regions of the southwestern United States and adjacent Mexico. Members of the genus are often conspicuous roadside weeds and are commonly known as paperflowers. In spite of their conspicuousness in the field, their suspected importance in livestock poisoning (Kingsbury, 1964; Schmutz, Freeman, and Reed, 1968), and their weedy nature, these species have remained poorly understood taxonomically.

Psilostrophe was first proposed by de Candolle (1838) from material collected by Berlandier from the vicinity of San Luis Potosi, Mexico. Three years later, the genus *Riddellia,* which would later prove to be synonymous with *Psilostrophe,* was erected by Nuttall (1841). *Riddellia* was typified by *R. tagetina* described from specimens collected by James in the Rocky Mountains. In 1849, A. Gray described a second species of *Riddellia, R. arachnoidea,* which he later realized (Gray, 1852, 1874) was the same as *Psilostrophe gnaphalodes.* Greene (1891) transferred the species of *Riddellia* to *Psilostrophe.* The first revisionary treatment of *Psilostrophe* came in 1903 when A. Nelson recognized six species. Rydberg (1914) reviewed the genus and named three additional species, bringing the total number of described species to ten. In the last comprehensive treatment of the genus, Heiser (1944) reduced the number of species to six. Heiser's work was revisionary and left room for a modern biosystematic study aimed at improving our understanding of the evolutionary relationships within *Psilostrophe,* which in turn provides the necessary background for further studies into adaptive strategies of species and roles of translocation heterozygosity, B-chromosomes, and polyploidy in the evolution of *Psilostrophe.*

Distributions and Habitats

Populations of *Psilostrophe* are common elements of the summer flora in North American deserts. All species are weedy under the right circumstances and certain of the species exhibit disjunct populations that probably represent recent introductions. The variable *P. tagetina* is the most widespread of the species and is found throughout much of New Mexico, southeastern Utah, extreme eastern Arizona, Texas, mostly west of the Pecos River, and south to the Mexican states of Chihuahua and Coahuila (Fig. 1). It occurs in desert shrub, prairie grasslands, and pinyon–juniper woodlands, often in sandy soils from 600 to 2400 m in

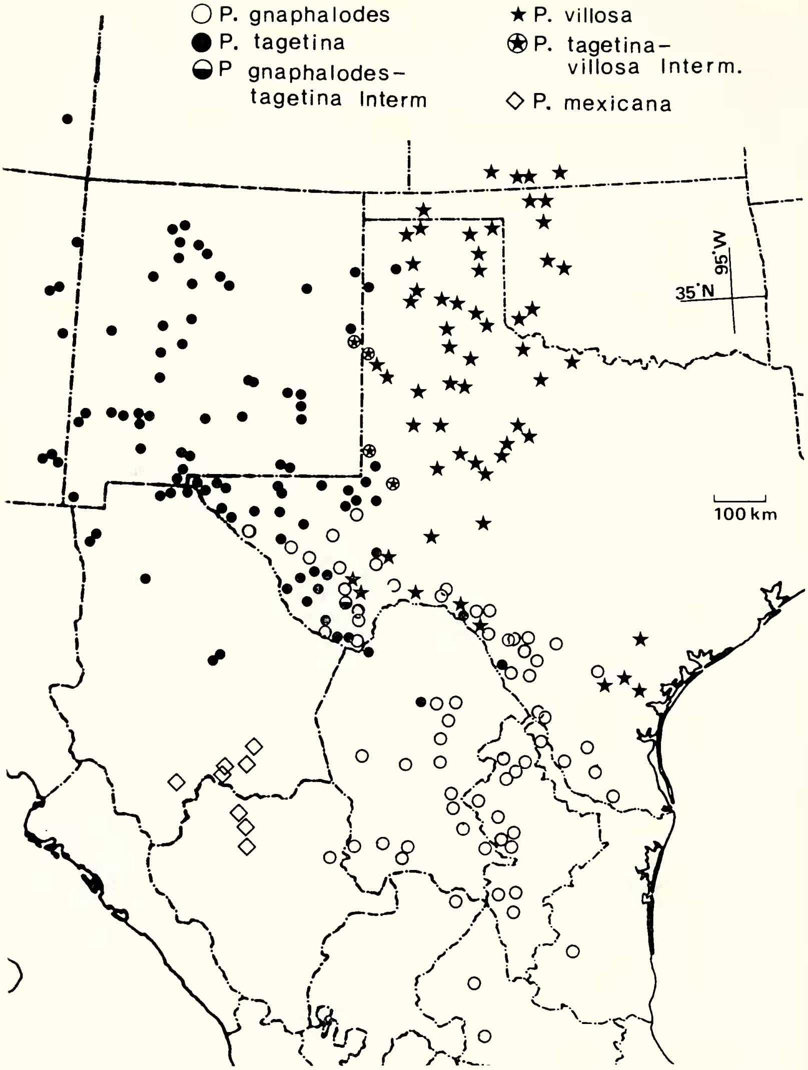

FIG. 1. Distributions of *Psilostrophe gnaphalodes, P. tagetina, P. gnaphalodes-P. tagetina* intermediates, *P. villosa, P. tagetina-P. villosa* intermediates, and *P. mexicana.*

elevation. The distribution of *P. tagetina* is overlapped by *P. gnaphalodes* and *P. villosa* in western Texas. Mixed populations containing *P. gnaphalodes* and *P. tagetina* occur in Brewster County, Texas. *Psilostrophe villosa* grows in prairie grassland from southwestern Kansas south to Texas at 300 to 900 m. *Psilostrophe gnaphalodes* grows in western Texas south to the Mexican state of San Luis Potosi from 300 to 2100 m. The remaining species with a Chihuahuan Desert distribution is the tetra-

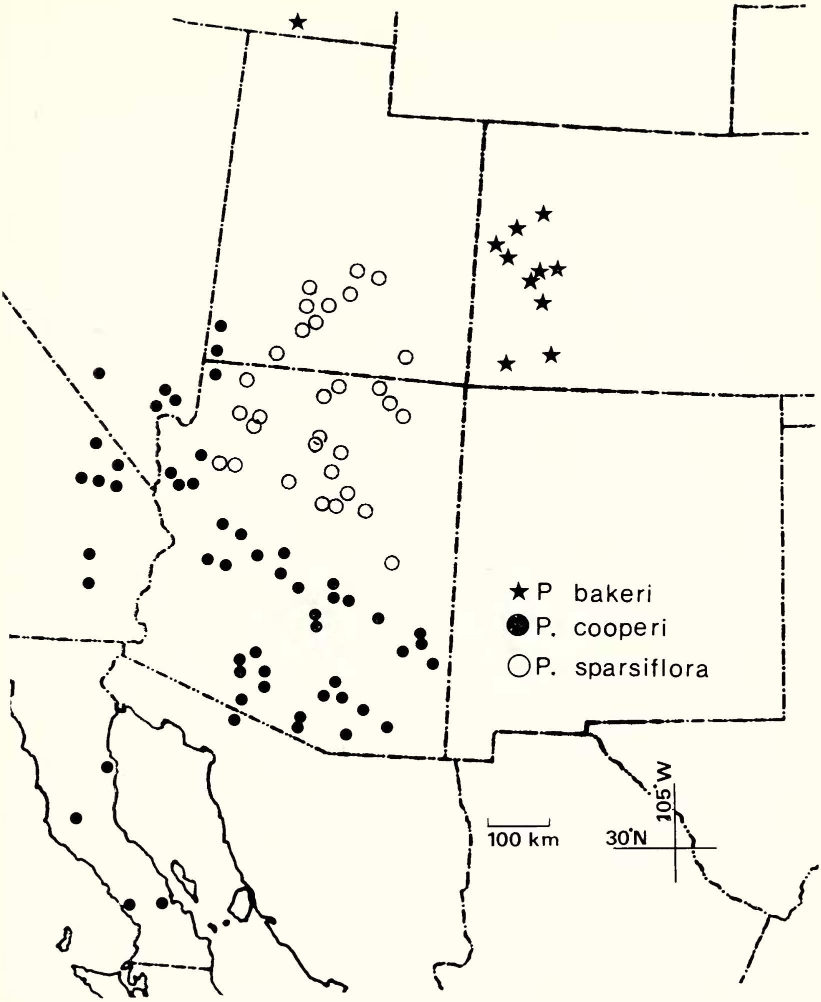

FIG. 2. Distributions of *Psilostrophe bakeri, P. cooperi,* and *P. sparsiflora.*

ploid, *P. mexicana.* It is encountered in hot desert shrubland to cool juniper woodlands in the states of Chihuahua and Durango, Mexico.

The three remaining species occur in or near the Mojave, Sonoran, and Great Basin Deserts (Fig. 2). *Psilostrophe cooperi* is encountered in the Mojave Desert and south and east to the northern Sonoran Desert in Arizona and Mexico along washes, rocky flats and hillsides, often in calcareous soils from 150 to 1500 m. *Psilostrophe sparsiflora* is generally found in sandy soils in sagebrush or pinyon–juniper communities in the cold Great Basin Desert from 900 to 2300 m. *Psilostrophe bakeri* is restricted to arid, rocky hills in western Colorado from 1350 to 2000 m and is disjunct in Idaho. Housing development and increased cultivation through irrigation threaten the habitat of this species.

HYBRIDIZATION EXPERIMENTS

A program of experimental hybridization was initiated to study the crossing relationships of the species. A total of 2318 pistillate florets were crossed in two years. Parental strains used were plants transplanted from their native habitats or collected as seed and grown to maturity in the greenhouse.

Capitula to be used as ovulate parents were emasculated by removal of the hermaphroditic disc florets prior to anthesis. Pistillate ray florets were then dusted with the pollen of the desired pollen parent. Heads of both pollen and seed parents were covered with glassine bags throughout the entire crossing procedure beginning with the bud stage to insure against possible contamination. After pollination the cross was tagged and allowed to mature under cover of the glassine bag. Achenes matured in about six weeks. Crossability is expressed as percent filled achenes following artificial hybridization. Estimates of parent and hybrid fertility were based on percent pollen stainability in aniline blue-lactophenol. At least 500 grains were counted wherever possible. Pollen stainability of parent plants ranged from 91 to 99 percent.

Intraspecific crossability was measured in interpopulational crosses in *P. cooperi, P. gnaphalodes,* and *P. tagetina* and ranged from 48 to 57 percent achene set, with an overall crossability of 51 percent (Table 1). Interfertility among species was variable, ranging from 0 to 53 percent achene set (Table 1; Fig. 3). Table 2 summarizes morphological features of the species. In general the hybrids were intermediate to the parental strains with respect to critical morphological characters. In all cases reflexed ligules were dominant to horizontal ligules in fruit. Other characters examined apparently were quantitatively inherited. Complete data on pollen stainability, morphology, and meiosis in individual parental and hybrid plants are found in Brown (1974).

When coupled with morphological and geographical evidence, the degree to which plants cross and produce vigorous hybrids and the degree of fertility of the F_1 offspring have long been used as indicators of genetic relationships of plants (Clausen, Keck, and Hiesey, 1941; Long, 1975). Crossability and fertility as determined in the greenhouse experiments are only of relative value and several limitations exist. Ability of species to cross in the greenhouse is a poor measure of their ability to hybridize in the field. Hybrids that apparently are vigorous in the greenhouse may not be competitive in the habitats of their parents. Furthermore, plants utilized in the experimental hybridizations represent only a minute sample of the total gene pool. That different plants in the same population may have different interspecific crossabilities is suggested by the crossing abilities of two individuals of *P. tagetina* collected from the same population in southeastern Arizona. All attempts

TABLE 1. CROSSABILITY IN *Psilostrophe*. [a]individuals/populations utilized.

Ovulate Parent	Pollen Parent	Total Ovules Crossed	% Achene Set Range
	INTRASPECIFIC CROSSES		
P. cooperi (3/3)[a]	*P. cooperi*	29	48 (38–52)
P. gnaphalodes (3/3)	*P. gnaphalodes*	37	57 (50–78)
P. tagetina (5/4)	*P. tagetina*	163	50 (46–78)
	INTERSPECIFIC CROSSES		
P. cooperi (5/3)	*P. sparsiflora* (1/1)	28	25 (19–50)
Reciprocal		26	0 (0)
P. cooperi (6/3)	*P. tagetina* (3/2)	45	7 (0–50)
Reciprocal		79	5 (0–13)
P. cooperi (4/3)	*P. villosa* (2/1)	24	0 (0)
Reciprocal		24	0 (0)
P. cooperi (3/3)	*P. bakeri* (1/1)	18	0 (0)
P. cooperi (2/1)	*P. gnaphalodes* (1/1)	55	29 (5–45)
Reciprocal		46	0 (0)
P. sparsiflora (4/2)	*P. tagetina* (4/3)	94	6 (0–23)
Reciprocal		50	6 (0–22)
P. sparsiflora (2/1)	*P. villosa* (2/1)	36	0 (0)
Reciprocal		21	0 (0)
P. sparsiflora (2/1)	*P. bakeri* (1/2)	23	4 (0–17)
P. sparsiflora (2/1)	*P. gnaphalodes* (3/3)	27	7 (0–22)
Reciprocal		98	4 (0–12)
P. tagetina (3/3)	*P. villosa* (2/1)	44	64 (44–72)
Reciprocal		24	42 (11–60)
P. tagetina (3/3)	*P. bakeri* (1/1)	43	21 (0–42)
P. tagetina (3/3)	*P. gnaphalodes* (3/3)	137	50 (36–77)
Reciprocal		195	44 (0–49)
P. villosa (1/1)	*P. bakeri* (1/1)	25	4 (4)
Reciprocal		20	0 (0)
P. villosa (1/1)	*P. gnaphalodes* (4/4)	35	26 (26)
Reciprocal		59	56 (33–69)
P. gnaphalodes (2/2)	*P. bakeri* (1/1)	30	0 (0)
	F_2 CROSSES		
P. cooperi × *sparsiflora*	*P. cooperi* × *sparsiflora*	only 1 plant flowered	
P. sparsiflora × *tagetina*	*P. sparsiflora* × *tagetina*	75	0
P. villosa × *tagetina*	*P. villosa* × *tagetina*	89	0
P. tagetina × *gnaphalodes*	*P. tagetina* × *gnaphalodes*	73	1
P. cooperi × *gnaphalodes*	*P. cooperi* × *gnaphalodes*	only 1 plant flowered	

Table 1, continued. Backcrosses

P. cooperi × *sparsiflora*	*P. sparsiflora*	16	6
Reciprocal		28	4
P. cooperi × *sparsiflora*	*P. cooperi*	9	0
Reciprocal		8	0
P. sparsiflora × *tagetina*	*P. sparsiflora*	61	0
Reciprocal		38	11
P. villosa × *tagetina*	*P. tagetina*	12	0
Reciprocal		29	0
P. villosa × *tagetina*	*P. tagetina*	82	37
Reciprocal		40	20
P. villosa × *tagetina*	*P. villosa*	—	—
Reciprocal		24	38
P. tagetina × *gnaphalodes*	*P. gnaphalodes*	53	6
Reciprocal		39	21
P. tagetina × *gnaphalodes*	*P. tagetina*	38	0
Reciprocal		38	0
P. cooperi × *gnaphalodes*	*P. gnaphalodes*	—	—
Reciprocal		20	0
P. cooperi × *gnaphalodes*	*P. cooperi*	11	0

Table 2. Summary of Morphological Similarities among Species of *Psilostrophe*.

	Vestiture			*Lower Lvs*			*Peduncles*			*Ligules*					*Achenes*		*Pappus*			
Species	Pilose	Villous	Pannose	Linear	Oblanceolate-	Spatulate	Short < 1 cm	Int. 1–5 cm	Long > 5 cm	Reflexed	Horizontal	Short < 6 mm	Int. 6–10 mm	Long > 10 mm	Villous	Glabrate	Erose	Lacerate	> ½ achene length	≤ ½ achene length
P. cooperi			+	+					+	+				+		+	+		+	
P. sparsiflora	+					+		+		+			+			+	+			+
P. bakeri		+				+		+			+			+		+	+		+	
P. tagetina		+				+		+			+		+			+	+			+
P. villosa		+				+	+				+	+				+	+			+
P. gnaphalodes		+				+	+				+		+		+			+		+
P. mexicana		+				+		+			+		+		+			+		+

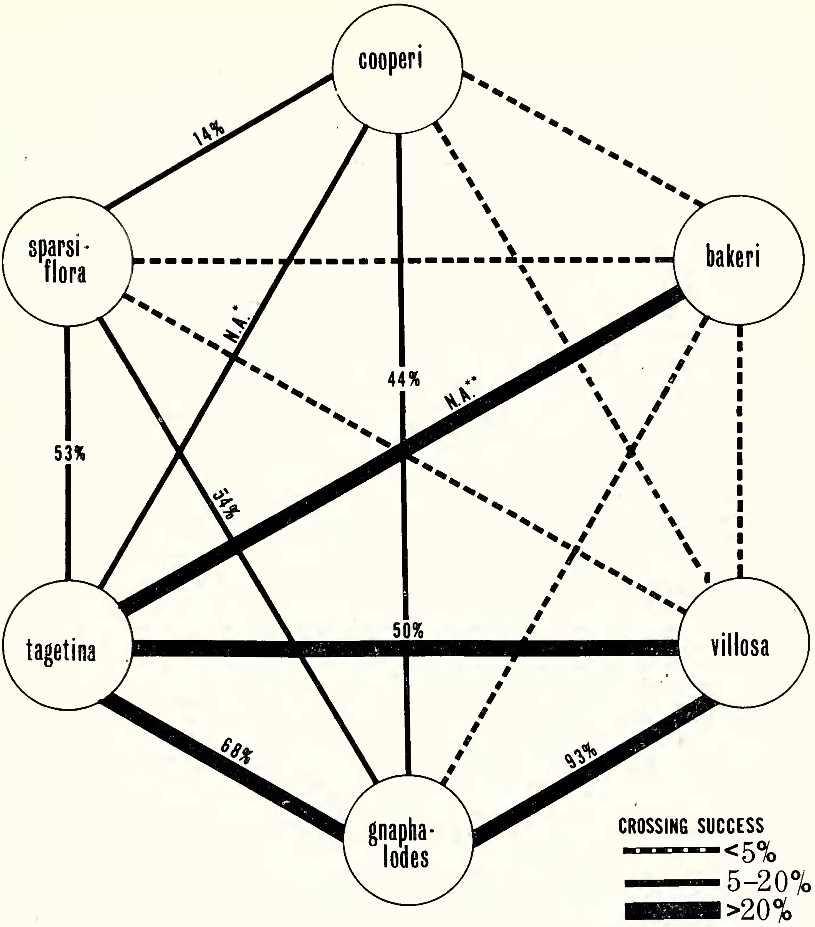

Fig. 3. Crossing diagram of the diploid species of *Psilostrophe* showing relationships based on percent interfertility. Mature F_1 hybrids were not obtained from crosses with less than 5 percent interfertility. Percentages above cross-bars indicate mean pollen stainability in F_1 hybrids (N.A.* = no data, achenes failed to germinate; N.A.** = no data, hybrids failed to flower).

to cross one individual with *P. sparsiflora* failed while attempts with the other were 23 percent successful (Brown, 1974). This suggests that all interspecific crossabilities would be higher if the ovulate parents were covered with pollen from a large number of plants (genotypes) as might occur under natural conditions. In addition, the backcrossing of F_1 hybrids to their immediate parents increases the likelihood of poor seed set due to the operation of possible sporophytic incompatibility systems. Recently, Jones (1976) presented evidence that environmental factors may exert a considerable influence on the production of stainable and presumed normal pollen. Nevertheless, data on crossability and pollen stainability in *Psilostrophe* seem in accord with morphological and geographical data.

Partial or complete internal barriers to gene exchange among species of *Psilostrophe* occur in the initial crossability and fertility of first-generation hybrids. Internal isolating mechanisms in *Psilostrophe* apparently are genic rather than chromosomal. Even though translocation heterozygosity is common in the genus, structural rearrangement has not been a major factor in speciation for interspecific hybrids possessed no more evidence of translocation heterozygosity than did their parents (Brown, 1977). In no case was evidence for inversions detected in the hybrids.

On the bases of morphology, geographical distribution, and crossing relationships, the diploid species of *Psilostrophe* fall into two categories: three distinct species in the Mojave, Sonoran, and Great Basin Deserts and a species alliance of *P. gnaphalodes–P. tagetina–P. villosa* in the southeastern portion of the range.

The southeastern species are very similar morphologically and are not always readily distinguishable. The ranges overlap considerably in western Texas, where intermediates occur. Artificial hybridizations showed initial crossabilities in any combination of these three species to be quite high (41 to 53 percent). Meiosis in the F_1 hybrids was regular with pollen stainability ranging from 44 to 93 percent. The interspecific hybrids showed an ability to backcross to either parent, but a marked inability to produce second generation plants. Limited gene flow between species seems possible in areas of sympatry and may provide an important source of genetic variability. Field studies of *Psilostrophe* in trans-Pecos Texas should contribute to an understanding of the extent and consequences of natural hybridization among these species.

The morphology and ecology of the tetraploid *P. mexicana* suggests that it is closely related to the *P. gnaphalodes–P. tagetina–P. villosa* diploid complex. *Psilostrophe mexicana* was recognized late in the study and its crossing relationships have not been studied. Without this information additional speculation on the phyletic relationships of this interesting taxon is unwarranted. Further work emphasizing artificial hybridization is needed to trace the origin of *P. mexicana*.

Psilostrophe bakeri, P. cooperi, and *P. sparsiflora* occur in specialized habitats in the northern and western portions of the genus range. Each species is ecologically and geographically distinct. Major morphological gaps involving several characters are suggestive of major genetic discontinuities among these three species. The three species are well isolated reproductively by low initial crossability in addition to external factors. Taxonomic decisions within this group are relatively simple and misidentification rare.

The species are allied genetically to *P. gnaphalodes* and *P. tagetina* of the southeastern alliance. Of 101 crosses attempted between *P. cooperi* and *P. gnaphalodes* 16 percent produced filled achenes. Six full achenes resulted from 125 hybridizations between *P. sparsiflora* and *P. gnaphalodes,* an overall crossability of 5 percent. Meiosis was regular in F_1 hybrids of either combination with 16 bivalents undergoing an orderly segregation (Brown, 1977). Pollen stainability ranged from 44 to 60 percent. Complete chromosomal pairing occurred in hybrids of species widely divergent in geography, ecology, and morphology. The overall weakness and low pollen fertility in the hybrids suggest some genetic disharmony.

Psilostrophe cooperi and *P. sparsiflora* showed much less crossing affinity to *P. tagetina:* 5 and 6 percent overall crossability respectively. These figures may be misleading for individuals of *P. tagetina* from the same population exhibited differing abilities to hybridize as mentioned earlier. None of the achenes resulting from crosses between *P. cooperi* and *P. tagetina* germinated. Pollen stainability in four hybrids between *P. sparsiflora* and *P. tagetina* ranged from 51 to 55 percent. Low hybrid fertility in attempts to produce an F_2 generation and backcrosses is evidence for internal isolation in addition to the eco-geographical isolation of these species.

Psilostrophe bakeri showed a 21 percent crossability with *P. tagetina* but little or no crossability with any other species. The simplest interpretation of this is to regard *P. bakeri* as derived from *P. tagetina* or its immediate ancestor. This distinct taxon is apparently reproductively as well as geographically isolated.

TAXONOMIC TREATMENT

The treatment of *Psilostrophe* is based on extensive field and herbarium studies in addition to studies of cytotaxonomy (Brown, 1977) and artificial hybridization. Most taxonomic difficulties in the genus arise because of substantial morphological similarities among the species. While in essential agreement with the capable revision of Heiser (1944), this study has brought to light additional characters useful in delimiting the species. A key to the species incorporating these characters is provided. In addition to reflecting increased knowledge about the geographical range and ecology of the species, this revision differs from that of Heiser in the recognition of *P. mexicana* and in the treatment of intraspecific variation in *P. tagetina.*

PSILOSTROPHE de Candolle, Prodr. 7:261. 1838. TYPE: *Psilostrophe gnaphalodes* de Candolle.

Riddellia Nuttall, Trans. Amer. Philos. Soc. n.s. 7:371. 1841. TYPE: *Riddellia tagetina* Nuttall.

Perennial or biennial, leafy-stemmed herbs. Stems simple below, clustered from a woody taproot often covered with old leaf bases, branching above. Leaves both rosulate and cauline or all cauline, alternate. Lower leaves spatulate to oblanceolate or linear, margins entire or pinnately lobed. Upper leaves much reduced, sessile and usually entire. Vegetative organs sparingly pilose to densely woolly or sometimes floccose. Capitula subsessile to long pedunculate, solitary or in corymbose clusters. Involucres cylindric; phyllaries 5–10, elliptic or lanceolate, herbaceous and uniseriate, or, if a second series is present, then the inner 1–7 bracts smaller than the outer and scarious. Corollas yellow to orange. Ray florets pistillate, fertile, 3–7 in a single series; the ligules becoming papery and persistent on the ripe achenes. Disc florets perfect, fertile; corolla tubes cylindric, the 5 triangular lobes glandular-pubescent without. Achenes terete or slightly angled, sublinear, conspicuously striate, glabrate to villous. Pappus of 4–6 nerveless, lanceolate, subequal, hyaline squamellae; the margins frequently erose, sometimes lacerate-dissected. Base chromosome number, $x = 16$.

KEY TO PSILOSTROPHE

Plants suffrutescent to subshrubby; pubescence of the stem densely white-pannose; lower leaves linear; heads scattered on peduncles 3–8 cm long . . . . 1. *P. cooperi*

Plants herbaceous; pubescence of the stem woolly to sparingly pilose; lower leaves spatulate to oblanceolate; heads in corymbose clusters, the peduncles less than 5 cm long.

Stems green, sparingly pilose, upper foliage glandular-dotted; ligules tightly reflexed against the involucre at maturity . . . . 2. *P. sparsiflora*

Stems loosely villous to white-woolly; ligules remaining horizontal in fruit.

Ray florets 5–6; disc florets 10–20; pappus scales less than one half the length of the disc corolla . . . . . . 3. *P. bakeri*

Ray florets 2–5; disc florets 5–12; pappus scales one half to equaling the disc corolla in length.

Achenes and pappus glabrate; pappus scales entire or merely erose.

Heads in open corymbs; peduncles 1–4 cm long; ligules 5-14 mm long, shallowly 3-lobed . . . . . 4. *P. tagetina*

Heads in congested corymbs; peduncles nearly wanting to 10 mm long; ligules 3–6 mm long, deeply 3-lobed . . . . 5. *P. villosa*

Achenes and pappus long-villous; pappus scales lacerate-dissected.

Heads in congested corymbs; peduncles nearly wanting to 10 mm long; disc corollas 3.5–4.0 mm long. 6. *P. gnaphalodes*

Heads in open corymbs; peduncles 8–30 mm long; disc corollas 4.5–5.0 mm long . . . . 7. *P. mexicana*

1. PSILOSTROPHE COOPERI (A. Gray) E. L. Greene, Pittonia 2:176.

1891.—*Riddellia cooperi* A. Gray, Proc. Amer. Acad. Arts 7:358. 1868.—Type: Gray cited the following specimens as representative, "Gravelly banks at Fort Mohave, Dec. 1861, *Dr. J. G. Cooper*. On the Colorado, *Dr. Newberry*. Camp Grant, &c., Arizona, *Drs. Elliot Coues* and *Edward Palmer*." Gray (1874) clearly stated that the species was first collected by Cooper, and Heiser (1944) designated the Cooper specimen (GH!) lectotype.

Perennial suffrutescent plants, 20–60 cm tall. Stems densely white-pannose, becoming less so with age, freely branched. Leaves cauline, lanate to glabrate, linear, entire, 1–8 cm long, less than 0.5 cm wide. Heads scattered, terminating the many branches; peduncles slender, 3–8 cm long. Involucres loosely to densely lanate, cylindric, 6–8 mm high and 3–5 mm in diameter. Corollas yellow. Ray florets 3–6, ligules 8–18 mm long and nearly as broad, 3-lobed, enlarging and becoming reflexed in fruit. Disc florets 10–25, corollas 4–5 mm long. Achenes glabrous to sparsely glandular with sessile glands; pappus scales oblong-lanceolate, entire to erose, obtuse to acute, less than ½ the length of the disc corolla. Chromosome number: $2n = 32$. Flowering throughout the year; mainly March to June.

2. Psilostrophe sparsiflora (A. Gray) A. Nelson, Proc. Biol. Soc. Wash. 16:23. 1903.—*Riddellia tagetina* var. *sparsiflora* A. Gray, Synopt. Fl. N. Amer. 1(2):318. 1884.—Type: Gray cited two specimens from southern Utah in his description of this variety. Heiser (1944) selected the specimen of Captain *Bishop s.n.* as lectotype (GH!).—*Psilostrophe tagetina* var. *sparsiflora* (A. Gray) E. L. Greene, Pittonia 2:176. 1891.

Psilostrophe divaricata Rydberg, North Amer. Flora 34:8. 1914.—Type: United States: Arizona: "Grand Canyon of the Colorado," 1897, *D. T. Allen s.n.* (Holotype, NY!; isotypes NY! UC!).

Perennial herbs, 10–50 cm high. Stems sparingly pilose to glabrate, single or clustered from a woody caudex, often twisted and zigzag at the nodes; freely branched, the branches more or less strongly divergent. Basal leaves rosulate, villous when young, becoming glabrate with age, spatulate to linear, up to 14 cm long, usually less than 1.5 cm wide, entire or rarely pinnately lobed, frequently lacking in mature specimens. Cauline leaves smaller, sparsely villous to glabrate, narrowly oblanceolate to linear, entire, acute to obtuse, dotted with sessile glands particularly near the inflorescence. Heads born in loose cymes of 3–6 on slender peduncles up to 3 cm long. Involucres lightly villous, cylindric, 5 mm high and 3 mm in diameter. Corollas yellow. Ray florets 1–4, often 2 or 3, ligules 6–10 mm long and decidedly broader, 3-lobed, enlarging and becoming sharply reflexed in fruit. Disc florets fewer than 10, corollas 3–5 mm long. Achenes glabrous to sparsely glandular with sessile glands; pappus scales lanceolate to linear, subequal, frequently erose, ½ to ⅔ the length of the disc corolla. Chromosome number: $2n = 32$. Flowering from April to October.

3. Psilostrophe bakeri E. L. Greene, Pl. Baker. 3:29. 1901.—Type: United States: Colorado: Montrose, *Baker 14* (NDG). Greene based his description of this species on two collections, *Baker 14* from near Montrose, Colorado and *Baker 106* from near Grand Junction, Colorado. Both collections are large gatherings with many duplicates and either could have provided the characters used in the diagnosis. In citing the type locality as Montrose, Colorado, Rydberg (1914), without stating his reason, implied that *Baker 14* is type, hence the specimen in the Greene Herbarium is designated as lectotype, (isolectotypes, GH! MO! POM! US!).

Riddellia tagetina var. *pumila* M. E. Jones, Proc. Calif. Acad. Sci. ser. 2, 5:700. 1895.—Type: United States: Colorado: Grand Junction, in gravel, in open places, 21 Jun 1894, *M. E. Jones 5474* (Lectotype here designated POM!; isolectotypes BM! MO! NY! POM! UC!).—*Psilostrophe pumila* (M. E. Jones) A. Nelson, Proc. Biol. Soc. Wash. 16:22. 1903.

Perennial herbs, 5–30 cm high. Stems long-villous, one to several from a branched woody caudex. Lower leaves rosulate, loosely villous, spatulate to oblanceolate, up to 8 cm long, entire or rarely pinnately 3- to 5-lobed. Cauline leaves smaller, oblanceolate, entire. Heads in loose corymbs at the end of the branches on peduncles 1.5–5.0 cm long. Involucres lightly villous, cylindric, 7–10 mm high and 4–6 mm in diameter; of 9 distinct bracts. Corollas yellow-orange. Ray florets 5–6, ligules 8–15 mm long and nearly as broad, 3-lobed. Disc florets 10–20, tubular corollas 4–5 mm long. Achenes glabrous, striate; pappus scales unequal, short erose, decidedly less than ½ the length of the disc corolla. Chromosome number: $2n = 32$. Flowering May to July.

4. Psilostrophe tagetina (Nuttall) E. L. Greene, Pittonia 2:176. 1891.—*Riddellia tagetina* Nuttall, Trans. Amer. Philos. Soc. n.s. 7:371. 1841.—Type: "The southern range of the Rocky Mountains, towards the sources of the Platte." Probably collected by Dr. James on Long's expedition (Gray, 1849) (Holotype BM!; isotype GH!). As pointed out by Heiser (1944) Nuttall's spelling in the original publication, "*Tagetinae*," was probably a misprint and subsequent workers have used the gramatically correct spelling, "*tagetina*."

Psilostrophe tagetina var. *lanata* A. Nelson, Proc. Biol. Soc. Wash. 16:21. 1903.—Type: United States: Texas: El Paso, Apr 1881, *G. R. Vasey s.n.* (Holotype US!).—*P. lanata* (A. Nelson) Hay, Miller & White, Proc. Biol. Soc. Wash. 16:186. 1903.

Psilostrophe hartmanii Rydberg, North Amer. Flora 34:8. 1914.—Type: Mexico: Chihuahua: near Laguna de Guzman, *C. V. Hartman 726* (Holotype NY!; isotype GH!).

Psilostrophe grandiflora Rydberg, North Amer. Flora 34:8. 1914.—TYPE: United States: Arizona: Cochise Co.: near Cedar Gulch, Paradise, 21 Sept 1907, *J. C. Blumer 1709* (Holotype NY!; isotypes FM! GH! MO! ARIZ! UC!).—*P. tagetina* var. *grandiflora* (Rydberg) C. B. Heiser, Ann. Missouri Bot. Gard. 31: 292. 1944.

Perennial herbs, 15–50 cm tall. Stems loosely to densely villous, becoming less so with age, clustered from the crown of a woody taproot or single-stemmed in the first year of growth, usually freely branched above, forming globose clumps. Lower leaves rosulate, loosely to densely white-villous, narrowly oblanceolate to more commonly spatulate, up to 15 cm long, less than half as wide, entire to pinnatisect with lanceolate to broadly linear segments. Upper leaves smaller, oblanceolate to linear, lightly villous, eglandular or nearly so. Heads terminating the many branches in open corymbs; peduncles 1–4 cm long. Involucres densely white-villous, 5–6 mm high and 2–4 mm in diameter. Corollas yellow to orange. Ray florets 3–6, commonly 3, ligules 5–14 mm long and usually noticeably broader, broadly 3-lobed at the apex. Disc florets 5–12, corollas 3-5 mm long. Achenes glabrous or with a few stout trichomes when young, striate, terete or slightly angled. Pappus scales broadly to narrowly lanceolate, acute to obtuse, one half to equalling the disc corolla in length. Chromosome number: $2n = 32$. Flowering May to October.

Nelson (1903) and Heiser (1944) have commented on the morphological diversity of this species. It is also variable cytologically (Brown, 1977). In addition to the typical form, two varieties, var. *lanata* and var. *grandiflora,* were recognized by Heiser (1944) and others. Both varieties are based on differences in size, particularly of the ligules and peduncles, and degree of pubescence, characters that are extremely variable. My observations lead me to believe that recognition of infraspecific taxa is unjustified. I have visited the type locality of var. *grandiflora* on several occasions and found the population to be morphologically and chromosomally variable. The type collection is definitely extreme in size. Comparable plants as to size of parts and degree of pubescence are uncommon. No cytological character such as translocation heterozygosity or number of supernumerary chromosomes could be correlated with any morphological character. Unless further investigations prove otherwise, I favor a conservative treatment of this variable and widespread species.

5. PSILOSTROPHE VILLOSA Rydberg in Britton, Manual Flora North. States Canada. 1006. 1901.—TYPE: Original description and illustration (no authentic type specimen located).

Psilostrophe cerifera A. Nelson, Proc. Biol. Soc. Wash. 16:21. 1903.—TYPE: "Cheyenne Country, Indian Territory." Jun 1891, *M. A. Carleton 201* (Holotype RM, paratype US!).

Psilostrophe cerifera var. *biennis* A. Nelson, Proc. Biol. Soc. Wash. 16:21, 1903.—TYPE: United States: Kansas: Meade Co.: prairie near Crooked Creek 16 Aug 1890, *B. B. Smyth 140* (Holotype US!, isotype NY!).—*P. biennis* (A. Nelson) Hay, Miller & White, Proc. Biol. Soc. Wash. 16:186, 1903.

Biennial or perennial herbs, 20–60 cm high. Stems loosely to densely long-villous, becoming less so with age. Basal leaves rosulate, densely long-villous, spatulate to oblanceolate, up to 10 cm long and less than 5 cm wide, entire or occasionally 3- to 5-lobed. Heads several at the ends of the branches in congested corymbs; peduncles subsessile to 5 mm long. Involucres densely white-woolly, 5–7 mm high and 3–4 mm in diameter. Corollas yellow-orange. Ray florests usually 3, ligules 3-6 mm long usually broader than long, deeply 3-lobed. Disc florets 5–10, corollas 3–5 mm long. Achenes glabrate; pappus scales linear-lanceolate, acute, one half to equaling the disc corolla in length. Chromosome number: $2n = 32$. Flowering from April to October.

6. PSILOSTROPHE GNAPHALODES de Candolle, Prodr. 7:261. 1838.—TYPE: Mexico: San Luis Potosi, *Berlandier 1336* (Holotype G, photographs FM! US!; isotype GH! probable isotypes BM! MO!).—*Riddellia gnaphalioides* (de Candolle) O. Hoffman in Loesner, Bull. Herb. Boissier 3:628. 1895.

Riddellia arachnoidea A. Gray, Mem. Amer. Acad. Arts ser. 2, 4:94. 1849.—TYPE: Three specimens are cited by Gray, "dry soil around Buena Vista and Saltillo, *Dr. Gregg, Dr. Wislizenus:* also near Monterrey, *Dr. Edwards.*" All three specimens are mounted on a single sheet in the Gray Herbarium. The Gregg specimen is here selected as lectotype (GH!).

Perennial herbs, 20–50 cm high. Stems loosely to densely villous, one to many from a woody taproot. Lower leaves rosulate, loosely to densely villous, spatulate to oblanceolate, up to 6 cm long and 1.5 cm broad, entire or occasionally pinnately 3- to 7-lobed. Upper leaves smaller, linear to oblanceolate, entire. Heads several at the ends of the branches in congested corymbose clusters; peduncles subsessile to nearly 1 cm long. Involucres densely white-woolly, 5–6 mm high and about 3 mm in diameter. Corollas yellow-orange. Ray florets 2–4, generally 3, ligules 4–7 mm long, usually slightly broader than long. Disc florets 5–9, corollas 3.5–4.0 mm long. Achenes and pappus scales long-villous, pappus scales linear-lanceolate, margins lacerate-dissected, about one half the length of the disc corolla. Chromosome number: $2n = 32$. Flowering throughout the year; mainly March to September.

7. PSILOSTROPHE MEXICANA R. C. Brown, Brittonia 26:115. 1974.—TYPE: Mexico: Chihuahua: desert shrub community dominated by *Larrea, Prosopis* and *Parthenium,* 8.1 mi N of junction to Jimenez along Hwy. 45, *Pinkava, McGill & Brown 788* (Holotype ASU!; isotypes to be distributed).

Perennial herbs, 15–50 cm tall, with one to many ascending, long-villous stems. Lower leaves rosulate, loosely to densely villous, oblanceolate to linear-oblanceolate in outline, entire or rarely lobed to subpinnatifid. Cauline leaves smaller, narrowly oblanceolate to linear. Heads several at the ends of the branches in open corymbs, peduncles 10–30 mm long. Involucre cylindric, woolly, 3–4 mm in diameter and 5–8 mm high. Corollas yellow-orange. Ray florets 3–5; ligules obovate to orbicular in outline, 5–8 mm long, 3-lobed. Disc florets 7–10; corollas 4.3–5.0 mm long. Achenes sublinear-oblong, long-villous with trichomes similar to those of the herbage; pappus scales lanceolate to linear, margins lacerate-dissected into long hairs. Chromosome number: $2n = 64$. Flowering from July to November.

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